Some Revision in Antechinus (Marsupialia)—2

By N. A. Wakefield* and R. M. Warneke**

SUMMARY

Antechinus stuartii is recognized as a species distinct from *A. flavipes,* and the taxonomy of the two is reviewed. It is shown that, in recent literature, the name *A. flavipes flavipes* has been misapplied to *A. stuartii.* A neotype is designated for *A. stuartii.*

Plastic and cranial characters of major populations of these species and of *A. godmani* are examined and compared statistically. The distribution of each is mapped.

A. flavipes flavipes, of temperate eastern Australia, and *A. f. leucogaster,* of south-western Australia, are animals of open dry sclerophyll forests, but two populations of the species in tropical Queensland are restricted to rainforest habitats.

A. stuartii stuartii occurs in dense dry sclerophyll and wet sclerophyll forests of the Eastern Highlands and coastal areas of south-eastern Australia. This habitat is essentially adjacent to that of *A. flavipes flavipes,* but the two species are sympatric in some places. The tropical race "*adustus*" belongs, not to *A. flavipes* but to *A. stuartii.*

An appendix shows a revised distribution of *Antechinus minimus maritimus.*

Taxonomy is revised as follows:

ANTECHINUS FLAVIPES

Antechinus flavipes flavipes

(*Phascogale flavipes* Waterhouse, 1837; north of Hunter River, New South Wales.)

South-eastern Queensland, New South Wales, Victoria, south-eastern South Australia.

(Subjective synonym: *Phascogale rufogaster* Gray, 1841; South Australia.)

Antechinus flavipes leucogaster

(*Phascogale leucogaster* Gray, 1841; Canning River, Western Australia.) South-western Western Australia.

Antechinus flavipes, populations of uncertain taxonomy.

North-east Queensland; Cape York Peninsula.

ANTECHINUS STUARTII

Antechinus stuartii stuartii

(*Antechinus stuartii* Macleay, 1841; Manly, New South Wales. Neotype: Waterfall, National Park, New South Wales.)

South-eastern Queensland, New South Wales, Victoria.

(Subjective synonyms: *Antechinus unicolor* Gould, 1854; Sydney, New South Wales. *Antechinus flavipes burrelli* Le Souef and Burrell, 1926; Ebor, north-eastern New South Wales.)

Antechinus stuartii adustus

(*Phascogale flavipes adusta* Thomas, 1923; Ravenshoe, north-eastern Queensland.)

North-eastern Queensland.

I. MATERIALS AND METHODS

(a) *Sources*

The sources of specimens and data are as follows:

American Museum of Natural History. (AMNH)

Australian Museum Sydney. (AM)

British Museum (Natural History). (BM)

Department of Zoology and Comparative Physiology, Monash University.

Division of Wildlife Research, C.S.I.R.O., Canberra.

Fisheries and Wildlife Department, Melbourne. (FWD)

Museum of Comparative Zoology, Harvard.

* Department of Zoology and Comparative Physiology, Monash University, Clayton, Victoria.

** Fisheries and Wildlife Department, Victoria.

National Museum of Victoria. (NMV)
Queensland Institute of Medical Research.
Queensland Museum, Brisbane.
Smithsonian Institution, United States National Museum.
South Australian Museum, Adelaide.
Western Australian Museum, Perth.

Although *Antechinus flavipes* and *A. stuartii* are widely distributed in eastern Australia and are abundant in areas of favourable habitat, both species are poorly represented in most museum collections. Of a total of about 250 specimens of *A. flavipes* and 400 specimens of *A. stuartii* examined, almost half are in the Fisheries and Wildlife Department collection.

In the course of the study, a programme of field observation and trapping was carried out, and, unless otherwise acknowledged, the details of habitat, set out in Sections III and VIII, are based on observations made by us in the course of that field work.

The other species dealt with in this paper, *A. godmani*, is known only from a small area in Queensland, and of the 37 specimens examined by us only 4 were available in Australian museums.

(b) *Characters examined and techniques of measurement*

The morphological features investigated and the techniques of measurement used were discussed in the previous paper of this series (Wakefield and Warneke, 1963). They are, in brief, as follows:

Characters examined

Size of body and appendages.
Size and morphology of the skull and teeth.
Characters of the pelage.
Characters of the feet.
External changes associated with breeding.

Techniques of measurement

Measurements of the body were taken using a measuring board, vernier calipers and a steel tape. The tail was measured from the cloaca; the pes from the heel to the tip of the longest toe, excluding the claw; and the ear from the tragoid notch to the tip.

While these techniques were used for all specimens in the Fisheries and Wildlife Department collection, they may not have been precisely the same as those used for measurements recorded with specimens from other institutions.

Figure 1 shows the seven measurements taken of the skull and dentition. The instruments used were either a HELIOS dial-reading or vernier calipers calibrated to 0.1 mm., and the measurements were taken with the aid of a binocular microscope at 6 to 10 magnifications. All cranial measurements recorded in this paper (except Thomas's of *A. godmani*) were made by this technique, and are recorded to the nearest 0·05 mm.

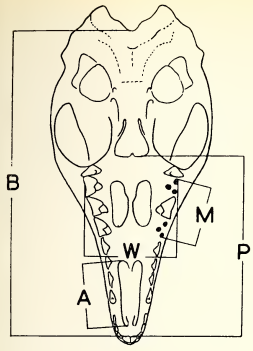
Specimens with milk teeth (deciduous fourth premolars) or in which the subsequent permanent premolars were not fully erupted were excluded from the tables of measurements.

(c) *Statistical analysis*

The "t" test, as outlined in Karmel (1959), was used for the comparisons, and the values of P were obtained from the statistical tables of Fisher and Yates (1957). Results are expressed in terms of the highest probability level exceeded (e.g. $P<0{\cdot}02$) of the range of probability levels 0·10, 0·05, 0·02, 0·01 and 0·001.

II. TAXONOMY OF ANTECHINUS FLAVIPES

The species was described by Waterhouse (1838) as *Phascogale flavipes,*



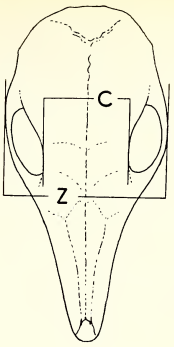


Fig. 1.
Skull measurements.
B—Basalar Length
Z—Zygomatic Width
C—Postorbital Constriction
P—Palatalar Length
A—Anterior Palatine Foramen
M—Alveolar Length M^{1-3}
W—Breadth at M^3

and the type, from "north of Hunter River, N.S.W.", is in the BM., No. 55.12.24.75 (skin and skull).

In recent literature—for example, Iredale and Troughton (1934) and Tate (1947: 127)—what we now regard as *Antechinus stuartii* (Sections VII-XI) has been identified as *A. flavipes flavipes*. But measurements and other details of the type specimen (communicated to us by R. E. Hill*), and Waterhouse's original description, identify the nominate form of *A. flavipes* according to our treatment of it in Sections III-VI.

Gray (1841) described a specimen from "Adelaide, South Australia" (BM. No. 41.1251; Skin and skull) as *Phascogale rufogaster*. Based on this, the trinomial *Antechinus flavipes rufogaster* has been used (Iredale and Troughton, *loc. cit.*; *et al.*) for a South Australian population of *A. flavipes*.

Gould (1863) did not confuse *A. flavipes* with *A. stuartii*. Of *A. flavipes* he stated: "I have observed it to be very abundant both in New South Wales and in South Australia", and remarked that "specimens from both countries presented little or no difference in size or colour". Our studies confirm this observation (Sections IV and V); the epithets *rufogaster* and *flavipes* apply to the one geographical race (Figure 2), and we regard *rufogaster* as a subjective synonym of *A. flavipes flavipes*.

Gray (*loc. cit.*) described another specimen, from "Canning River, Western Australia" (BM. No. 41.1244), as *Phascogale leucogaster*. This represents a population that is currently recognized (Iredale and Troughton, *loc. cit.*) as *A. flavipes leucogaster*. It is geographically isolated (Figure 2), and our comparisons (Sections III and IV) indicate that this subspecific status is justified.

While there has been sufficient material available to provide a reasonably clear picture of *A. flavipes* in the temperate region, the relatively few specimens available from northern Australia have allowed no such clarification of the status of its tropical populations. The population of North-east Queensland probably warrants separate subspecific status, and that of Cape York certainly does. Correct taxonomic procedure in the latter case will not be clear until ample comparative material

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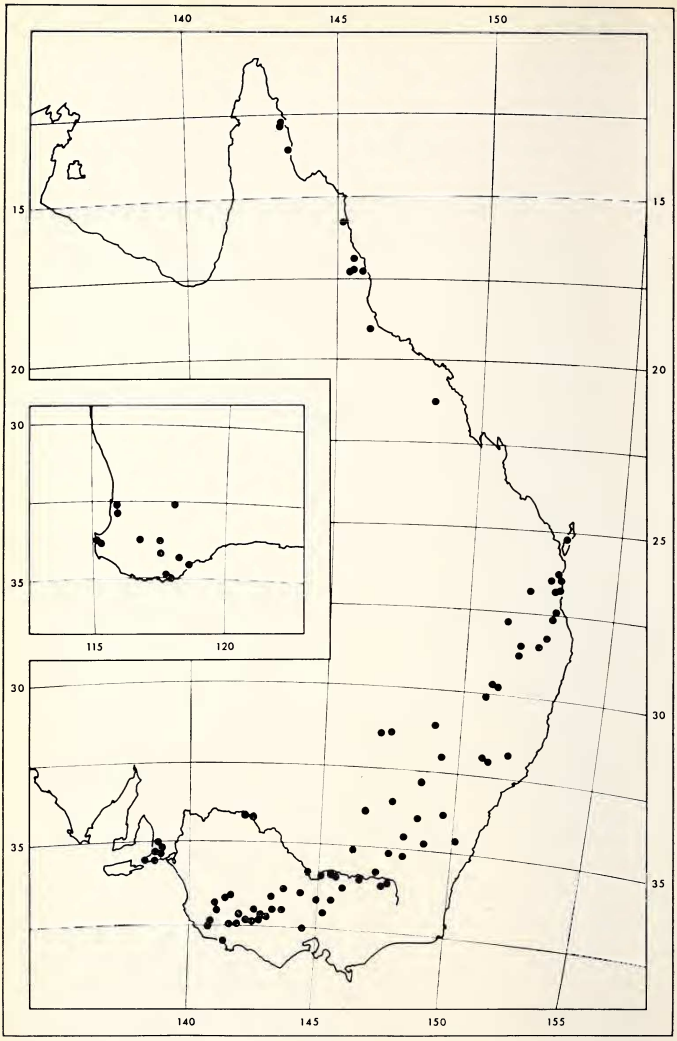


Fig. 2. Distribution of *Antechinus flavipes*.

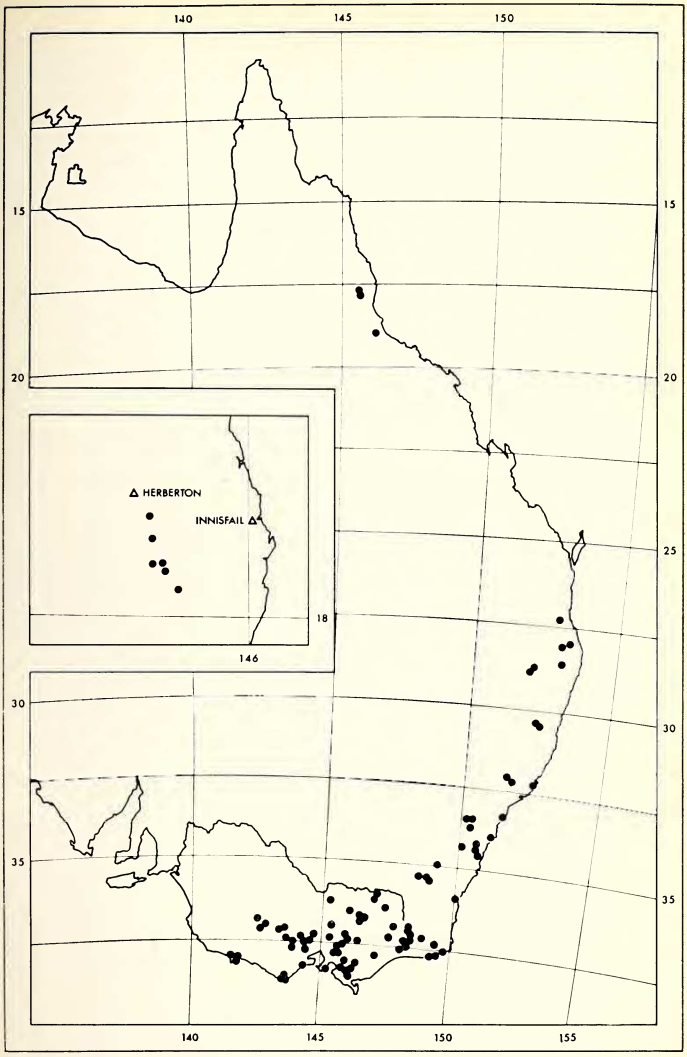


Fig. 3. Distribution of *Antechinus stuartii*, and (inset) of *A. godmani*.

is available of the Arnhem Land animal which Thomas (1904) named *Phascogale bella.*

(The names *Antechinus unicolor, A. flavipes burrelli* and *A. flavipes adustus* are excluded from the synonymy of *A. flavipes*; they belong to that of *A. stuartii* (Section VII).)

III. DISTRIBUTION AND HABITAT OF ANTECHINUS FLAVIPES

The main population, which comprises the nominate race, *A.f. flavipes,* is found in south-eastern Queensland, eastern New South Wales, Victoria and south-eastern South Australia (Figure 2). It is mainly on the inland side of the Great Dividing Range but is near-coastal at both the northern and south-western extremities of its distribution.

The habitat is fairly open forest, mainly in areas of rainfall between 15 and 25 inches per annum. According to the classification of Wood and Williams (1960), the areas occupied are partly dry sclerophyll forest and partly woodland.

Krefft (1866) reported *A. flavipes* as abundant in 1857 in the woodlands of Black Box (*Eucalyptus bicolor*) and Red Gum (*E. camaldulensis*) of the Murray River flood plains, from Echuca to Mildura. Its distribution along that river evidently linked the Adelaide-Mount Lofty Range population with that of Victoria and New South Wales.

At least in Victoria, most trees with which the species is associated are fibrous-barked eucalypts, either "box" species or "stringy-barks". Food, comprising insects mainly, is obtained from the trunks and large limbs of these trees and about logs. The animals are almost wholly nocturnal and crepuscular, but individuals are occasionally seen abroad in full daylight.

Homes, for daytime refuge, are normally hollow logs and hollow trunks of trees. Specimens caught at Glenlofty (western Victoria) were living in the trunk of a Red Stringybark (*Eucalyptus macrorrhyncha*), with Yellow Box (*E. melliodora*) and Long-leaf Box (*E. goniocalyx*) in association as well as scattered logs and a sparse ground cover of saw-sedge (*Gahnia radula*) and tussock grass (*Poa*) (Figure 4). In the lower Glenelg district (south-western Victoria) the habitat was Brown Stringybark (*E. baxteri*) and Messmate (*E. obliqua*), with a few logs and an abundance of bracken (*Pteridium esculentum*) and tussock grass. In the Grampians (western Victoria) the species commonly occupies crevices in sandstone cliffs, and along the lower Glenelg River it occasionally inhabits holes in limestone outcrops.

The Western Australian race, *A.f. leucogaster,* is recorded mainly from forests of Jarrah (*Eucalyptus marginata*) and Tuart (*E. gomphocephala*), in the Perth-Blackwood-Albany area.

The habitats of both the North-east Queensland population and that of Cape York Peninsula are tropical rainforests. The former is recorded from Mount Finnegan, Speewah, Russell River and Innisfail; the latter is from McIlwraith Range (Rocky Scrub), Tozer Range, Iron Range and upper Nesbit River. The habitat of each of these localities has been described by Brass, (1953).

IV. PLASTIC CHARACTERS OF ANTECHINUS FLAVIPES

Both Jones (1923) and Finlayson (1958), using South Australian material and thus avoiding confusion with *A. stuartii,* have given accurate accounts of *A. f. flavipes* (under the synonym, however, of *A. f. rufogaster*). Taken together, their notes provide a very detailed description of the external morphology of the form.

A. flavipes is a lithe, compactly built animal of shrew-like rather than murine form. The tail is shorter than the head-body length and is not incrassated. The ears, thin in substance, are comparatively large and conspicuous when fully erect but may be folded against the head when the animal is alarmed. The pes, like those of squirrels (Sciuridae), are capable of a considerable degree of rotation, which, together with the prominent and strongly ridged pads on the manus and pes, are features of other members of the Dasyuridae with pronounced scansorial habits.

In the past, much emphasis has been placed on plastic characters in the description of subspecies. The variation observed and measured in each of the geographically isolated populations of *A. flavipes,* as shown in Figure 2, is given below.

(a) *Body measurements*

Details of body measurements, and of numbers of specimens from which these were taken, are set out in Tables 1-4. The figures for *A. f. flavipes* do not include data of any Queensland specimens, but apply only to material from New South Wales, Victoria and South Australia.

In these tables, the average figures for tail, ear and pes lengths have been expressed as percentages of head-body length. These percentages indicate that body proportions are essentially the same for each of the eastern Australian series, as well as for the two sexes within each series.

For most of the specimens from North-east Queensland and Cape York (i.e. those in the AMNH), the ear had been measured from the crown, instead of the tragoid notch. In several instances both measurements were recorded.

Fig. 4. Habitat of *Antechinus flavipes* and *A. stuartii,* Glenlofty, Victoria.

Table 1

Body measurements of *Antechinus flavipes flavipes* (south-eastern Australia)
Measurements in millimetres

		Range	Mean±S.E.	Standard deviation
Head–body	23 ♂♂	101 –135	116·2±2·46	11·80
	16 ♀♀	94 –120	107·9±2·14	8·57
Tail	23 ♂♂	70 –112	95·0±2·44 *(82%)	11·72
	18 ♀♀	78 – 96	86·9±1·09 (81%)	4·65
Ear	23 ♂♂	14·5– 21	18·9±0·39 (16%)	1·86
	18 ♀♀	13 – 20	17·5±0·41 (16%)	1·72
Pes	25 ♂♂	18 – 22	20·4±0·21 (18%)	1·04
	18 ♀♀	17 – 20	18·7±0·24 (17%)	1·02

* Per cent of head–body length.

Table 2

Body measurements of *Antechinus flavipes leucogaster* (south-western Australia)
Measurements in millimetres

		Range	Mean±S.E.	Standard deviation
Head–body	4 ♂♂	100 –108	105·3±1·87	3·74
	9 ♀♀	86 –104	94·9±1·77	5·30
Tail	4 ♂♂	73 – 94	85·3±4·44 *(81%)	8·87
	9 ♀♀	65 – 80	73·1±1·49 (77%)	4·46
Ear	4 ♂♂	17 – 18	17·3±0·25 (16%)	0·50
	9 ♀♀	15 – 18	16·3±0·66 (17%)	1·97
Pes	4 ♂♂	18 – 20	19·3±0·48 (18%)	0·96
	9 ♀♀	16 – 18	16·8±0·22 (18%)	0·67

* Per cent of head–body length.

and these, together with "notch" measurements for the remainder of the series, indicate that the difference between the two is of the order of 5 mm. For the sake of uniformity "crown" measurements were converted to "notch" by the addition of this length.

Sexual dismorphism of the order of about 8 per cent is apparent in all linear measurements save that of ear length, but sufficient data for statistical evaluation were available only in the case of *A. f. flavipes* and the Cape York form of the species. In both forms the difference in pes length was statistically significant, with $P<0{\cdot}001$ in both cases. In head-body and tail length, Cape York males were significantly larger than females ($P<0{\cdot}001$) but in the tests of *A. f. flavipes* the highest probability levels exceeded were only 0·02 and 0·01 respectively.

From the tables it can be seen that the Cape York form is approximately

TABLE 3

Body measurements of *Antechinus flavipes* from North-east Queensland
Measurements in millimetres

		Range	Mean ± S.E.	Standard deviation
Head–body	5 ♂♂	121 –145	131·0 ± 4·03	9·03
	8 ♀♀	108 –136	119·4 ± 3·79	10·72
Tail	5 ♂♂	100 –114	107·2 ± 2·39 *(82%)	5·36
	8 ♀♀	83 –105	93·5 ± 3·13 (78%)	8·86
†Ear	5 ♂♂	19 – 21	19·4 ± 0·40 (15%)	0·90
	7 ♀♀	16 – 19	17·3 ± 0·60 (15%)	1·60
Pes	5 ♂♂	21 – 24	22·6 ± 0·59 (17%)	1·33
	8 ♀♀	19 – 23	20·9 ± 0·45 (18%)	1·27

* Per cent of head–body length.
† "Crown" measurement +5 mm.

TABLE 4

Body measurements of *Antechinus flavipes* from Cape York Peninsula, Queensland
Measurements in millimetres

		Range	Mean ± S.E.	Standard deviation
Head–body	40 ♂♂	118 –154	140·0 ± 1·03	6·57
	27 ♀♀	108 –140	122·4 ± 1·52	7·92
Tail	40 ♂♂	101 –133	118·8 ± 1·00 *(85%)	6·33
	26 ♀♀	91 –110	100·7 ± 0·87 (82%)	4·46
†Ear	39 ♂♂	16 – 20	18·1 ± 0·16 (13%)	0·97
	25 ♀♀	16 – 19	18·0 ± 0·17 (15%)	0·87
Pes	40 ♂♂	23·5– 27	25·0 ± 0·15 (18%)	0·93
	25 ♀♀	21 – 24	22·4 ± 0·18 (18%)	0·92

* Per cent of head–body length.
† "Crown" measurement +5 mm.

20 per cent longer in head-body, tail and pes length than is *A. f. flavipes*. The data on the North-east Queensland form are less reliable, but they indicate that it is intermediate in size between the Cape York form and *A. f. flavipes*. As the figures for *A. f. leucogaster* show it to be about 10 per cent small r than *A. f. flavipes*, it is apparent that a well-defined clinal gradient in body size exists, with the largest form at the northern extremity and the smallest form at the south-western extremity of the species' arc-like range.

(b) *Manus and pes*

The normal appearance of the palmar and plantar surfaces of the feet of *A. flavipes* is shown in Figure 5. In all specimens examined the first interdigital (pollical) and inner metacarpal pads on the manus were well

TABLE 5

Fusion of first interdigital pad with inner metacarpal pad on manus and with inner metatarsal pad on pes in *Antechinus flavipes*, *A. stuartii* and *A. godmani*

	Fusion on both feet		Fusion on one foot		Fusion on neither foot	
	N	%	N	%	N	%
flavipes (manus)	—	—	—	—	21	100
stuartii „	—	—	3	3	98	97
godmani „	—	—	—	—	26	100
flavipes (pes)	1	5	1	5	19	90
stuartii „	78	77	13	13	10	10
godmani „	11	42	4	16	11	42

separated, but in Jones (1923: 96) an illustration of the palm of *A. f. flavipes* shows the inner metacarpal lacking or fused with the first interdigital. This is apparently a rare occurrence.

In Figure 5 the inner metatarsal pad of the pes is shown distinctly separate from the first interdigital pad (hallucal). However in some specimens these pads were in contact or, more rarely, fused (see Table 5). This latter condition was noted on the pes of two specimens from Victoria.

In *A. flavipes* the granulations on the palm and sole are not pigmented as in *A. swainsonii* (see Wakefield and Warneke, 1963: 202) and are therefore less obvious. However in most specimens of *A. flavipes* we have seen, several conspicuously large granules were noted between the outer metatarsal pad and the heel, as can be seen in Figure 5. In most cases there were two, in others none, one or three.

(c) *Pelage*

A. flavipes flavipes. The main pile is dense and moderately soft, but a profusion of long, coarse guard hairs imparts a rather crisp texture to the coat. There is marked antero-posterior differentiation in dorsal colour: the head and foreparts are dark grizzled grey and the lower back and rump are suffused with buff or reddish fawn. This toning is a composite effect due to an intermingling of several discrete colours in the fur. The dominant colour of the main pile is confined to a broad band between a basal zone of deep slate grey and an extreme terminal zone of dark brown to black; it is white on the head and shoulders and a rich ochraceous buff on the rump. A grizzled effect is produced by the interspersed guard hairs which are wholly black or tipped with light brown.

The flanks, ventrum and inner side of the limbs are in marked contrast, as guard hairs are lacking and the colour in the fur (ochraceous buff to golden tan) extends from the basal zone of slate grey right to the tip of each hair. The inguinal and gular areas are less brightly coloured.

Orbital crescents of light buff, and a patch of buff fur at the base and to the back of each ear, are very conspicuous. The ears are sparsely clothed with short adpressed buff hairs, some at the lower part of the conch being dark terminally. The dorsal surfaces of manus and pes are buff to ochraceous buff, undiluted by darker elements.

The tail is clothed with short ad-

pressed hairs which tend to mask rings of small epidermal scales underneath. Above it is buff, grizzled with black, becoming wholly black at the apex where the hairs are noticeably longer. Below it is deep buff, darkening towards the apex.

These notes on the pelage of *A. flavipes flavipes* were compiled after examination of a large series of skins from South Australia, Victoria, New South Wales and south-eastern Queensland. For the most part these specimens agreed well with descriptions of both the type, from north-eastern New South Wales (Waterhouse, 1838), and the South Australian population (Jones, 1923: 95-6; and Fin-

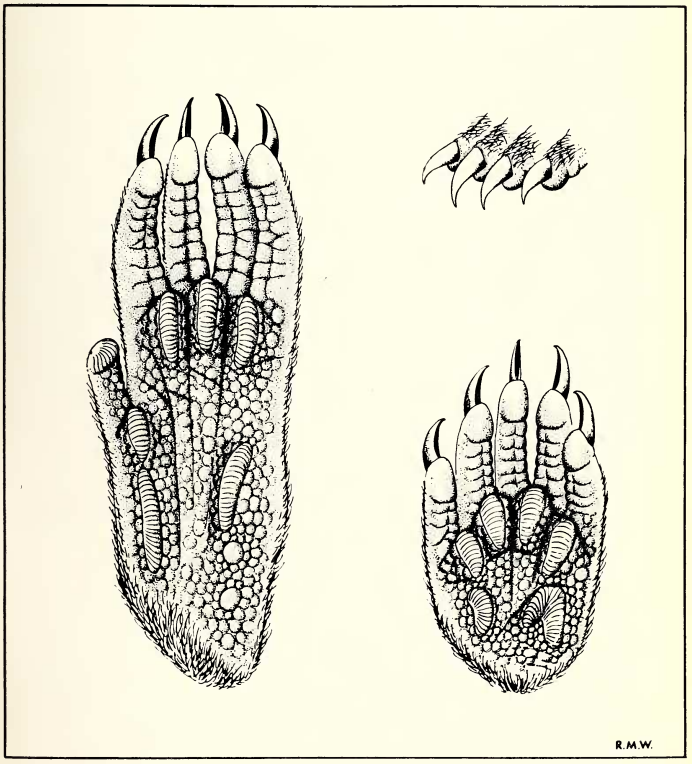
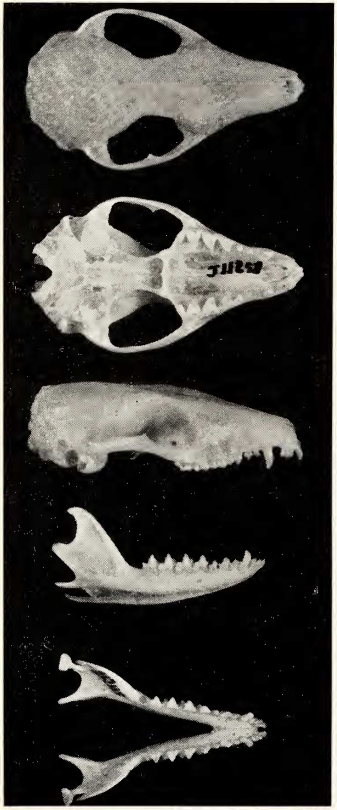
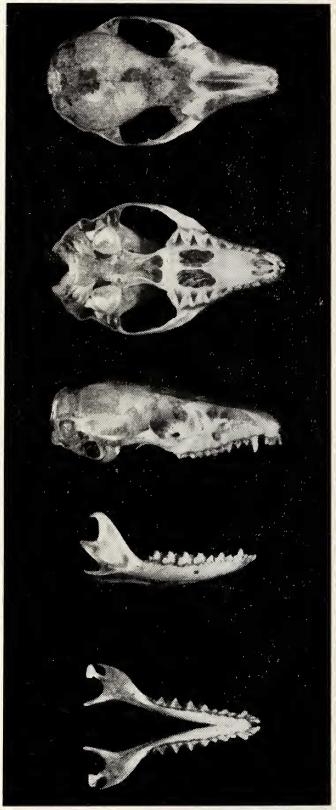


Fig. 5. Foot characters of *Antechinus flavipes*.
Left—Left pes. *Lower right*—Left manus. *Upper right*—Foreclaws.

layson, 1958: 145). However, in certain localities variants do occur, but only to the extent of a reduced intensity of the colour of the lower back, flanks and ventrum, to a pale buff. This was noted in single specimens from various localities and in whole series from certain Queensland localities: Imbil (26°28′ S., 152°41′ E.), Barney View (28°15′ S., 152°47′ E.), and Frazer Island (at about 25° S.) off the coast.



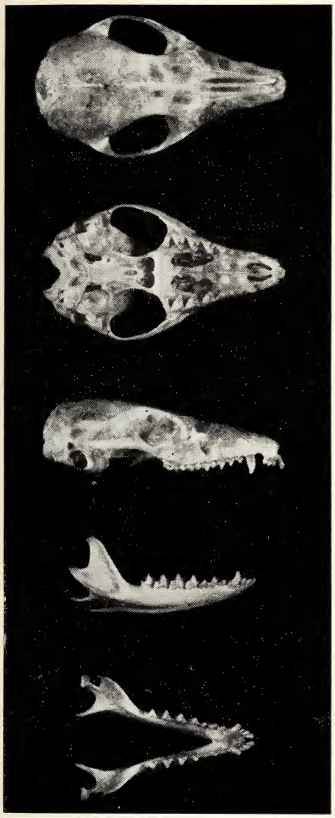


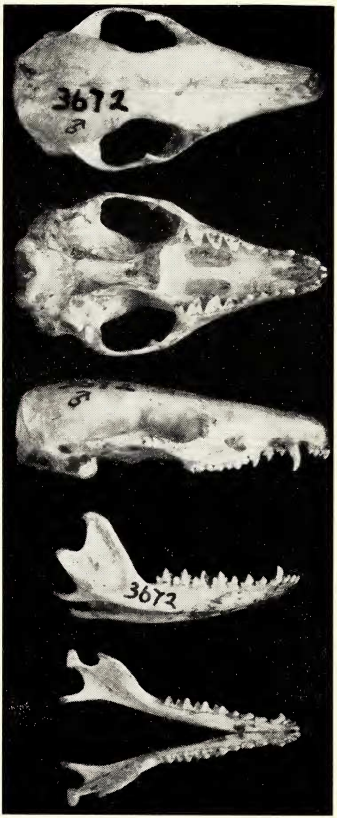
Photos: *J. Cooper, FWD.*

Fig. 6. Skull and mandible of an adult male *Antechinus flavipes flavipes* from Frazer Island, S.E. Queensland. (Queensl. Mus., No. J.11258).

Fig. 7. Skull and mandible of an adult female *Antechinus flavipes leucogaster* from Kalamunda, W. Aust. (FWD, No. D.642).

A. flavipes leucogaster. In the Western Australian animal the bright ochraceous tonings of the typical form are replaced by a subdued and sombre ochraceous brown. However, the physical components of the pelage and the pattern of colours are essentially the same in all respects save one; the ochraceous brown of the flanks does not extend across the ventrum. In ventral aspects, white-tipped fur extends from the gular to the in-





Photos: *J. Cooper, FWD.*

Fig. 8. Skull and mandible of the neotype of *Antechinus stuartii stuartii*, an adult male from Waterfall, National Park, N.S.W. (AM, No. M.5294).

Fig. 9. Skull and mandible of an adult male *Antechinus godmani* from Evelyn, N. Queensland (Queensl. Mus., No. J.3672).

TABLE 6

Cranial measurements of *Antechinus flavipes flavipes*

Measurements in millimetres

		Range	Mean ± S.E.	Standard Deviation
Basalar length (B.L.)	45 ♂♂	25·75–30·80	28·09 ± 0·21	1·408
	26 ♀♀	23·45–28·20	25·80 0·17	0·866
Zygomatic breadth (Z.B.)	48 ♂♂	16·15–20·40	18·34 ± 0·15	1·032
	28 ♀♀	15·75–18·35	16·81 0·12	0·620
Postorbital constriction (P.C.)	49 ♂♂	5·90– 7·05	6·52 ± 0·04	0·273
	30 ♀♀	5·95– 7·20	6·36 0·05	0·291
Palatalar length (P.L.)	50 ♂♂	13·80–16·80	15·29 ± 0·11	0·761
	30 ♀♀	12·75–15·30	14·24 0·09	0·510
Anterior palatine foramen	50 ♂♂	2·25– 3·70	2·89 ± 0·04	0·294
	29 ♀♀	2·25– 3·05	2·71 0·05	0·250
Breadth at M^3 (B.M.)	50 ♂♂	9·45–11·10	10·27 ± 0·06	0·422
	30 ♀♀	9·10–10·60	9·80 0·06	0·334
Length, M^{1-3}	51 ♂♂	5·40– 6·50	5·87 ± 0·03	0·210
	34 ♀♀	5·30– 6·20	5·70 0·05	0·304
P.C./B.L., as per cent	42 ♂♂	19·6 –25·6	23·2 ± 0·21	1·33
	26 ♀♀	22·4 –26·6	25·4 0·32	1·63
Z.B./B.L., as per cent	43 ♂♂	62·1 –68·7	65·3 ± 0·25	1·60
	25 ♀♀	61·9 –67·4	64·9 0·35	1·78
P.L./B.L., as per cent	43 ♂♂	52·4 –56·7	54·4 ± 0·14	0·92
	26 ♀♀	52·6 –57·7	55·0 0·23	1·19
B.M./B.L., as per cent	44 ♂♂	34·0 –39·0	36·7 ± 0·17	1·11
	26 ♀♀	34·8 –40·0	38·0 0·23	1·16
P.C./Z.B., as per cent	48 ♂♂	30·8 –39·2	35·6 ± 0·30	2·06
	28 ♀♀	34·8 –41·2	37·8 0·30	1·58

guinal region and onto the inner side of the limbs. The whiteness is variably modified by the basal colour of slate grey showing through.

North-east Queensland series. The dorsal colour pattern of specimens from this region is the same as that of *A. f. flavipes*, with strong antero-posterior differentiation and overtones of black due to the guard hairs. The head and shoulders are dark, lightly tinged with brownish buff, and the lower back and rump are a warm rust brown. The latter colour is especially bright on the flanks where the guard hairs are lacking, but on the ventrum it is much reduced in intensity and is further diluted by a grey undertone due to a basal zone of slate grey.

Orbital crescents and ear patches of brown or brownish buff are inconspicuous in some specimens. The dorsal surface of both manus and pes is brownish buff. The tail is darker above as in the typical form but with darker tones of brown corresponding with those of the body fur, and is dark brown to black at the apex.

Cape York series. The pelage of specimens from this region is quite distinct. The pile is of shorter length and is more coarse than that of *A. f. flavipes* even though the guard hairs are less strongly developed, and be-

TABLE 7

Cranial measurements of *Antechinus flavipes leucogaster*
Measurements in millimetres

		Range	Mean±S.E.	Standard deviation
Basalar length (B.L.)	8 ♂♂	25·50–27·70	26·56±0·30	0·846
	10 ♀♀	23·40–26·55	24·79 0·28	0·886
Zygomatic breadth (Z.B.)	9 ♂♂	16·00–19·50	17·40±0·33	0·984
	10 ♀♀	14·70–17·40	15·83 0·25	0·794
Postorbital constriction (P.C.)	10 ♂♂	5·85– 6·60	6·32±0·09	0·270
	13 ♀♀	5·80– 6·30	6·15 0·04	0·143
Palatalar length (P.L.)	11 ♂♂	13·75–15·00	14·40±0·13	0·414
	12 ♀♀	13·00–14·55	13·58 0·11	0·374
Anterior palatine foramen	13 ♂♂	2·50– 3·10	2·82±0·05	0·195
	16 ♀♀	2·20– 3·25	2·65 0·07	0·286
Breadth at M^3 (B.M.)	11 ♂♂	9·30–10·20	9·68±0·08	0·276
	12 ♀♀	8·75– 9·65	9·20 0·08	0·284
Length, M^{1-3}	11 ♂♂	5·20– 5·80	5·43±0·05	0·180
	13 ♀♀	5·15– 6·00	5·42 0·06	0·215
P.C./B.L., as per cent	8 ♂♂	22·9 –25·2	23·8 ±0·29	0·82
	10 ♀♀	23·7 –26·2	24·8 0·23	0·74
Z.B./B.L., as per cent	8 ♂♂	62·7 –70·4	65·3 ±0·82	2·33
	9 ♀♀	60·5 –65·5	63·3 0·62	1·86
P.L./B.L., as per cent	8 ♂♂	53·5 –55·4	54·3 ±0·24	0·67
	10 ♀♀	53·8 –55·5	54·9 0·16	0·51
B.M./B.L., as per cent	8 ♂♂	35·4 –37·6	36·5 ±0·31	0·86
	10 ♀♀	35·8 –39·1	37·0 0·36	1·29
P.C./Z.B., as per cent	9 ♂♂	33·3 –39·3	36·6 ±0·64	1·91
	10 ♀♀	36·2 –42·3	38·8 0·63	2·00

cause the guard hairs are not prominent the fur over the head and shoulders has not the cold tones which are characteristic of the southern and western forms already described; antero-posterior differentiation is slight and indistinct. The general appearance is of slightly grizzled pale brown over the whole dorsum, scarcely warmer with a tinge of rust brown on the rump, and pale brown on the flanks, ventrum and inner side of the limbs. The basal zone of the main pile is everywhere slate grey.

Orbital crescents are absent and ear patches are not differentiated, other than by the absence of darker elements which are present in the adjacent fur. The dorsal surface of both manus and pes is fawn. The colours of the upper and under surfaces of the tail correspond with the adjacent body fur, darkening to brown or occasionally black at the apex.

V. SKULL AND DENTITION OF ANTECHINUS FLAVIPES

For its size the skull is quite massively constructed; it is broad across the zygomatic region, is of moderate depth, and has a short conical rostrum (see Figures 6 and 7). Features of particular significance are the relatively narrow postorbital constriction (narrower in relation to zygomatic

breadth in mature animals than in the young), absence of postorbital processes, and short anterior palatine foramina. The alisphenoid bulla is inflated and rounded in form while the "mastoid" portion, which is almost entirely enclosed by the periotic, is scarcely so.

The teeth are robust and powerful. I^1 is at least twice the bulk of I^2, is cylindrical or very slightly flattened laterally, markedly proödont and separated from I^2 by a wide diastema. I^{2-4} are crowded together with their triangular crowns overlapping; $I^2>I^3>I^4$. The upper canine is a broad tapered peg, slightly curved. $P^4>P^3>P^1$, with P^1 at least twice the bulk of P^1. There is no metaconic projection at the rear of M^4. The lower incisors are semi-recumbent; $I_1>I_2>I_3$. The lower canine is short, with a distinct posterior basal ledge. $P_3>P_1>P_4$.

The deciduous premolar dP^4, which is lost early in life, is a tiny low-crowned molariform tooth with three roots. By comparison, dP_4 is even smaller, being less than half its bulk. It is similar to the permanent premolars in form but is proportionately broader at the base and has a much lower crown. It has two roots which may be either divergent or contiguous.

A summary of seven cranial measurements and five skull proportions of each of the four geographically isolated populations is set out in Tables 6-9. Using the "t" test, the three variants have been compared statistically with the typical form.

A. f. leucogaster. According to Tate (1947: 128) this is a "thoroughly good race with larger bullae and smaller teeth than any of the east Australian races". A cursory examination of the average values of the skull proportions in Table 7 is sufficient to show that *A. f. leucogaster* is virtually identical to *A. f. flavipes* in the form of the skull, but in all the linear measurements taken it is of smaller size. Most of these linear differences from the typical form are not of high statistical significance, but in the case of breadth at M^3 both male and female *A. f. leucogaster* are quite distinctly smaller than the typical form ($P<0{\cdot}001$ for both tests).

In all morphological features the dentition of the two forms is essentially the same.

North-east Queensland series. Again, the skull proportions of this form differ to only a minor degree from those of the typical form. From the few specimens measured, males average about the same size and females slightly larger in skull size than their southern counterparts. There is not, however, a skull measurement common to both sexes which sets the North-east Queensland form apart from *A. f. flavipes.*

Cape York series. Skulls from this region were the largest seen; the average dimensions of the female series exceeding, in most measurements, those of the series of *A. f. flavipes* males. The statistical significance of the lineal differences between these two forms were all of high order. On the other hand the two forms are closely similar in skull proportions. The greatest difference, in the proportion Z.B./B.L. (Table 9), does suggest that the Cape York form is narrower in the zygomatic region, but statistically this difference is not significant.

Sexual dismorphism. The most obvious sexual differences in the skull were those of length and width. In *A. f. flavipes, A. f. leucogaster* and in the Cape York form, differences in

Comparison of *Antechinus stuartii* and *Antechinus flavipes*

Above: *A. stuartii*, ♂, Glenlofty, Victoria (FWD, No. DY.417).
Below: *A. flavipes*, ♂, near Nelson, Victoria (FWD, No. DY.409).

(Note: In the lower picture the normal grey component of face and back coloration has been rendered bluish by the photography.)

basalar length, palatalar length and zygomatic breadth were found to be of high statistical significance ($P<0.001$), but in the small series from North-east Queensland no appreciable sexual dimorphism in the skull was demonstrated.

The length of the anterior palatine foramen was a remarkably constant feature between the sexes of each of the four populations. Postorbital constriction, molar row and breadth at M^3 are not influenced by sex to any marked degree, except in *A. f. flavipes* and *A. f. leucogaster* where males are significantly broader at M^3.

When *A. flavipes* is considered in terms of its distribution along the Eastern Highlands and west across southern Australia, several anatomical trends are apparent. The most obvious is skull size (length and breadth), the largest occurring in Cape York Peninsula and the smallest in south-western Western Australia. A second and related trend can be seen in the length of the tooth row (see also Tate, 1947: 126-7). The average alveolar length of M^{1-3} of the South Australian series examined by us was 5.95 ± 0.04 mm.

Tate (1947: 126), in discussing the *A. flavipes* group (in which he included *A. stuartii* and *A. godmani*), described an ascending gradient in relative bulla size from the Papuan region through north Queensland to south and finally south-western Australia. This slight trend was apparent in the complex of the four populations of *A. flavipes* examined in this paper (see Figures 6 and 7).

VI. BREEDING CONDITION OF ANTECHINUS FLAVIPES

Females. In the non-breeding condition the pouch area is scarcely differentiated, its site on the lower abdomen being indicated by a small patch of rather coarse hairs of a uniform light fawn colour. Nipple counts made on females in this condition are difficult and unreliable as the nipples are quite minute and do not project from the skin.

As breeding is restricted to a short period each year and the populations are low at that time, relatively few females showing signs of breeding activity are represented in museum collections and, unfortunately, not all of them are dated. However, those with reliable data indicate that in Victoria the young are born in early August (NMV. No. R.12784), while in north Queensland they are born between mid-August and early September (AMNH series). No data on the Western Australian population were available.

In Victoria, lactation continues through to mid-November at least, by which time the young are no longer carried by the mother (FWD. No. D.233). In this specimen the mammary area was large and conspicuous, being devoid of hair and stained reddish brown. Its lateral margins were marked by raised ridges of skin and anteriorly it was bordered by a conspicuous fringe of long reddish hairs. Six pairs of elongated nipples were arranged symmetrically, parallel to the lateral margins.

In *A. flavipes* the nipple number is variable. In the Western Australian form satisfactory counts were obtained from only two specimens, both of which had 10. In the typical form the number is 10 or 12, and either may be noted in females from the same locality. Only two reliable counts from North-east Queensland were available, both of which were 8. Counts made on Cape York females were of either 10 or 8 nipples, but most of the latter were recorded with a query.

TABLE 8

Cranial measurements of *Antechinus flavipes* from North-east Queensland
Measurements in millimetres

		Range	Mean ± S.E.	Standard Deviation
Basalar length (B.L.)	9 ♂♂	25·95–31·35	28·29 ± 0·50	1·490
	9 ♀♀	26·15–28·70	26·42 0·45	1·340
Zygomatic breadth (Z.B.)	9 ♂♂	17·00–19·60	18·37 ± 0·28	0·835
	9 ♀♀	16·70–19·00	17·60 0·22	0·658
Postorbital constriction (P.C.)	9 ♂♂	6·50– 7·30	6·80 ± 0·08	0·250
	10 ♀♀	6·00– 7·20	6·73 0·12	0·369
Palatalar length (P.L.)	9 ♂♂	13·90–17·05	15·25 ± 0·33	0·984
	9 ♀♀	14·35–15·70	14·79 0·17	0·517
Anterior palatine foramen	9 ♂♂	2·40– 3·20	2·82 ± 0·09	0·254
	10 ♀♀	2·40– 3·00	2·71 0·06	0·187
Breadth at M^3 (B.M.)	9 ♂♂	9·50–11·25	10·19 ± 0·20	0·587
	9 ♀♀	9·85–10·90	10·40 0·12	0·359
Length, M^{1-3}	9 ♂♂	5·40– 6·20	5·86 ± 0·11	0·315
	10 ♀♀	5·60– 6·50	5·98 0·09	0·279
P.C./B.L., as per cent	9 ♂♂	22·0 –25·8	24·1 ±0·37	1·12
	10 ♀♀	22·4 –27·0	24·5 0·66	1·15
Z.B./B.L., as per cent	9 ♂♂	61·6 –70·4	65·0 ±0·85	2·54
	10 ♀♀	62·0 –66·2	64·4 0·49	1·56
P.L./B.L., as per cent	9 ♂♂	52·2 –55·2	53·3 ±0·41	1·22
	10 ♀♀	53·2 –55·7	54·8 0·23	0·74
B.M./B.L., as per cent	9 ♂♂	34·1 –37·2	36·2 ±0·33	0·98
	10 ♀♀	36·0 –39·3	37·9 0·31	1·00
P.C./Z.B., as per cent	9 ♂♂	35·2 –39·4	37·1 ±0·53	1·60
	10 ♀♀	35·9 –40·7	38·1 0·43	1·48

Males. In other *Antechinus* dealt with by us (Wakefield and Warneke, 1963: 208), the only external sign of sexual maturity in males was the size of the testes, considerable enlargement occurring some weeks before pouch development in the females. Our observations on live Victorian specimens indicate that this is also the normal pattern of development in male *A. flavipes*.

VII. TAXONOMY OF ANTECHINUS STUARTII

Macleay (1841) published both the genus *Antechinus* and the specific epithet *stuartii* as novelties to describe a male specimen from Spring Cove (i.e. Manly), New South Wales. In the original diagnosis the number of upper incisors was given as 6, but this was later corrected by a note (Macleay, 1842) stating that the dental formula was the same as that of *Phascogale*.

The original description was made from the notes of "J. Stuart, Esq.", and it was stated that the specimen had been lost. However, Macleay's later note indicated that he had examined a (the?) skeleton. As recent endeavours to locate this skeleton in the Macleay Museum, Sydney, and elsewhere, have been unsuccessful,

TABLE 9

Cranial measurements of *Antechinus flavipes* from Cape York Peninsula, Queensland
Measurements in millimetres

		Range	Mean ± S.E.	Standard Deviation
Basalar length (B.L.)	39 ♂♂	29·00–32·65	30·38 ± 0·17	1·048
	20 ♀♀	26·75–29·50	28·14 0·18	0·787
Zygomatic breadth (Z.B.)	38 ♂♂	17·80–20·50	19·17 ± 0·10	0·590
	21 ♀♀	16·60–18·85	17·67 0·15	0·704
Postorbital constriction (P.C.)	41 ♂♂	6·35– 7·35	6·90 ± 0·03	0·217
	26 ♀♀	6·25– 7·20	6·72 0·04	0·212
Palatalar length (P.L.)	40 ♂♂	15·60–17·85	16·68 ± 0·09	0·569
	27 ♀♀	14·90–16·50	15·52 0·06	0·326
Anterior palatine foramen	41 ♂♂	2·45– 3·55	3·00 ± 0·05	0·298
	27 ♀♀	2·40– 3·55	2·90 0·05	0·266
Breadth at M^3 (B.M.)	40 ♂♂	10·25–11·70	10·91 ± 0·05	0·290
	27 ♀♀	9·75–11·15	10·55 0·06	0·317
Length, M^{1-3}	42 ♂♂	5·85– 6·75	6·13 ± 0·03	0·182
	28 ♀♀	5·80– 6·30	6·04 0·03	0·135
P.C./B.L., as per cent	39 ♂♂	20·0 –24·5	22·5 ± 0·16	0·98
	20 ♀♀	22·5 –26·1	24·0 0·20	0·89
Z.B./B.L., as per cent	37 ♂♂	59·3 –66·0	62·8 ± 0·23	1·37
	17 ♀♀	60·8 –66·0	62·9 0·36	1·48
P.L./B.L., as per cent	39 ♂♂	52·8 –55·9	54·5 ± 0·14	0·89
	20 ♀♀	53·0 –56·9	55·0 0·21	0·96
B.M./B.L., as per cent	38 ♂♂	33·2 –38·0	35·6 ± 0·19	1·17
	20 ♀♀	36·4 –38·9	37·7 0·17	0·78
P.C./Z.B., as per cent	38 ♂♂	32·4 –38·5	35·9 ± 0·23	1·44
	21 ♀♀	34·3 –41·4	38·3 0·41	1·88

we conclude that the type specimen is indeed lost.

As a neotype we have selected a male specimen in the Australian Museum, No. M5294 (spirit specimen and skull), collected at Waterfall, National Park, New South Wales, on August 7, 1932. Its measurements in mm. are as follows: head-body 101, tail 94, ear 17 and pes 18; of the skull: basalar length 26·30, zygomatic breadth 16·90, postorbital constriction 6·95, palatalar length 14·70, anterior palatine foramen 2·75, breadth at M^3 9·50, and length of M^{1-3} 5·50.

Our reasons for accepting that Macleay's *Antechinus stuartii* is, in fact, the species we treat as such in this paper, and not any other eastern New South Wales phascogalinid, are as follows:

1. The large size (total length 9½ inches) excludes members of the *murina-leucopus* group of *Sminthopsis,* and size together with the comparatively long tail ("cauda fere corporio longitudinem aequante") also excludes *S. crassicaudata.*
2. The pelage colour ("fulvus abdomine artubusque subtus albescentibus"), and the coastal habitat, exclude *Antechinus flavipes.*
3. The comparatively long tail excludes *Antechinus swainsonii.*

4. The tail features ("cauda teres pilosa gracilis") excludes *Phascogale tapoatafa*.

Gould (1854) described *Antechinus unicolor* from New South Wales (BM. No. 54,11.19.2). The plate is an accurate portrayal of the almost concolorous *Antechinus stuartii*. One of Gould's specimens, a female, like Macleay's original, is of greater size than any example of *A. stuartii* measured by us (see Table 10).

Le Souef and Burrell (1926) described *Antechinus flavipes burrelli* from Ebor, north-eastern New South Wales. The type specimens (AM. No. M.2593), and others from that locality, are of *A. stuartii*, and they do not demonstrate any feature which would justify subspecific status. Ebor is within the geographical range of what we regard as the nominate form of *A. stuartii* (see Figure 3); hence *"burrelli"* is treated as a subjective synonym of *A. stuartii stuartii*.

Iredale and Troughton (*loc. cit.*) misapplied the trinomial *Antechinus flavipes flavipes* to the central-eastern New South Wales population which is, in fact, the nominate form of *A. stuartii*. This error has been perpetuated in many subsequent publications dealing with that population (Troughton, 1941; Tate, 1947; Horner and Taylor, 1959; Marlow, 1961; etc.).

Thomas (1923) established the trinomial *Phascogale flavipes adusta* for specimens of *Antechinus* from Ravenshoe in the Atherton area of north-eastern Queensland. Measurements of these, communicated to us by R. E. Hill, including the type specimen (BM. No. 22.12.18.54), and the original diagnosis, show that *"adusta"* belongs, not to *A. flavipes*, but to *A. stuartii*. Thomas himself later realized that two species were involved, designating one *"flavipes"* and the other *"unicolor"* on his specimen labels; *"adusta"* he placed with *"unicolor"* (W. D. L. Ride*, *in litt.*, 12.x.1965).

Not having examined sufficient specimens of this tropical population of *A. stuartii*, we are unable to assess its status. The average body and cranial measurements of 5 males and of 2 females that are given in Table 12 at least demonstrate that it is comparable in size and form to *A. stuartii stuartii* (see Table 10). The population appears to be geographically isolated (see Figure 3) and can be distinguished as *A. stuartii adustus*, pending more knowledge of its morphology and distribution.

The distribution of *A. stuartii* overlaps that of *A. flavipes* in several areas. The two have been shown to be truly sympatric by the trapping of typical specimens of each at (a) Glenlofty, western Victoria (37°04′ S., 143°12′ E.), and (b) "Stoney Creek", midway between Murrumbateman and Gundaroo, south-eastern New South Wales (35°00′ S., 149°09′ E.), the latter by P. Woolley, A.N.U., Canberra. This evidence of reproductive isolation supports our action in recognizing the two forms as distinct species.

VIII. DISTRIBUTION AND HABITAT OF ANTECHINUS STUARTII

The nominate race, *A. s. stuartii*, extends from the extreme south-east of Queensland, through eastern New South Wales and eastern and central Victoria, to the extreme south-west of Victoria. In this area it occurs in the highlands about the Great Dividing Range and in the coastal tracts between the highlands and the sea.

Essentially, its area of distribution is on the coastal side of that of *A. f. flavipes*; the ranges of the two are complementary, with little overlap. On the other hand, the general range of

* Director, Western Australian Museum.

A. s. stuartii is practically the same as that of *A. swainsonii mimetes* (see Wakefield and Warneke, 1963, Figure 2), and these two are commonly sympatric.

A. s. stuartii occupies a comparatively wide variety of habitats within the general categories of wet sclerophyll forest and dry sclerophyll forest. Rainfall on these habitats ranges from about 25 to over 60 inches per annum, and the elevations are from sea level to at least 4500 feet. Our observations suggest that this species is the most abundant marsupial in south-eastern Australia.

At Loch Valley the rainfall is about 56 inches per annum, and the natural vegetation is a forest of White Mountain Ash (*Eucalyptus regnans*), with a mid-storey of Silver Wattle (*Acacia dealbata*) and some Myrtle Beech (*Nothofagus cunninghamii*), and a dense under-storey of shrubbery and ferns. In a similar habitat, in the Marysville area of east-central Victoria, several specimens were caught in traps placed about 20 feet above the ground on limbs of Silver Wattle trees.

Specimens of *A. stuartii* were found in a fairly open forest of Snow Gum (*Eucalyptus pauciflora*) at 4500 feet elevation, in the upper Buchan River area (eastern Victoria); they were identified as *A. flavipes* (Wakefield, 1960). In the same district, at about 3000 feet near Mount Seldomseen, examples were trapped in a dense forest of Broad-leaf Peppermint (*Eucalyptus dives*), Messmate (*E. obliqua*) and Silver Wattle, with numerous logs and much low shrubbery.

In coastal dune scrubs at Mallacoota (eastern Victoria) the main trees of the habitat are Gum Myrtle (*Angophora intermedia*), banksias (*Banksia integrifolia, B. marginata*), Bracelet Honey-myrtle (*Melaleuca armillaris*), with bracken and several shrub species of the heath family (*Epacridaceae*). In the same district, specimens were caught in runways of bush rats (*Rattus fuscipes assimilis*) in an area almost devoid of trees, under a dense ground cover of Spear Grasstree (*Xanthorrhoea hastilis*) and numerous sedge species (*Cyperaceae*) and grasses.

At Mount Clay near Portland (south-western Victoria) the habitat is fairly open forest of stringybark eucalypts (*E. baxteri, E. obliqua*) with fallen logs and a dense ground cover of bracken, Dwarf She-oak (*Casuarina*), flat-pea (*Platylobium*), Flame Heath (*Astroloma conostephioides*) and speargrass (*Stipa muelleri*). The population of *A. stuartii* in this general area was cited by Finlayson (1958) as the "Heathmere variant" of *A. flavipes*. In the Gorae Forest, west of Mount Clay, *A. stuartii* has been caught within 10 miles of the lower Glenelg habitat of *A. flavipes* (see Section III), but the ranges of the two species have not been found to overlap in this district.

In the Ballarat district (western Victoria), with a rainfall of 27 inches per annum, there is a comparatively pale variant of *A. stuartii* in forests of Narrow-leaf Peppermint (*E. radiata*) and Messmate, with a light ground cover of tussock-grass (*Poa*), some bracken and scattered clumps of Small Grasstree (*Xanthorrhoea minor*). Homes are made in hollow limbs and trunks of the peppermint trees, and many nests have been found in stacks of firewood that have been left in the bush for two or three years to dry. The nests are of leaves and bark.

The Glenlofty habitat, where *A. stuartii* and *A. flavipes* are sympatric, is described in Section III. A single specimen of *A. stuartii* was trapped there amongst tussock-grass and sawsedge (*Gahnia radula*) which provided a 50 per cent ground cover on a nar-

TABLE 10

Body measurements of *Antechinus stuartii stuartii* (total series)
Measurements in millimetres

		Range	Mean±S.E.	Standard Deviation
Head–body	123 ♂♂	77 –121	97·4±0·70	7·80
	63 ♀♀	74 –120	91·2 1·18	9·29
Tail	119 ♂♂	73 –109	94·1±0·73 *(97%)	7·99
	67 ♀♀	65 – 99	84·3 0·91 (92%)	7·50
Ear	109 ♂♂	13·5– 19	15·9±0·12 (16%)	1·28
	73 ♀♀	13·5– 19	15·9 0·18 (17%)	1·51
Pes	126 ♂♂	15·5– 19·5	17·9±0·08 (18%)	0·89
	78 ♀♀	14 – 20	16·9 0·12 (18%)	1·06

* Per cent of head–body length.

TABLE 11

Body measurements of *Antechinus stuartii stuartii* (Loch Valley series)
Measurements in millimetres

		Range	Mean±S.E.	Standard Deviation
Head–body	58 ♂♂	77 –107	95·3±0·85	6·49
	13 ♀♀	76 – 93	84·9 1·45	5·23
Tail	56 ♂♂	80 –108	98·0±0·75 *(103%)	5·64
	13 ♀♀	78 – 99	87·5 1·73 (103%)	6·23
Ear	58 ♂♂	13·5– 17	15·4±0·11 (16%)	0·87
	13 ♀♀	14 – 16·5	15·0 0·21 (18%)	0·75
Pes	58 ♂♂	16 – 19·5	17·7±0·13 (19%)	0·98
	13 ♀♀	15 – 17	16·1 0·23 (19%)	0·82

* Per cent of head–body length.

row strip of flat ground along a dry water course. It had a pale pelage typical of the Ballarat variant (see Plate). Specimens of *A. flavipes* were caught 65 yards to the south, 260 yards to the east, and about half a mile to the west and south respectively of the locus of the *A. stuartii* specimen, some in traps placed about logs within the margin of the sedge-grass flat. In addition to the eucalypts previously mentioned, the Candlebark Gum (*E. rubida*) occurred at that spot (Figure 4).

The Grampians population of *A. stuartii* is within the geographical range of *A. flavipes,* and both species are distributed generally in these mountains. A specimen of *A. stuartii* and one of *A. flavipes* were trapped at the same spot, about 2 miles west of Mount Frederick, but at different times.

Troughton (1941) gave details of *A. stuartii* inhabiting crevices in the sandstones of the Sydney area, though he identified it as *A. flavipes,* and he commented on the agility of the ani-

TABLE 12

Antechinus stuartii adustus: average body and cranial measurements of 5 males and of 2 females

Measurements in millimetres

	♂♂	♀♀		♂♂	♀♀
Head–body	109·2	100·0	Anterior palatine foramen	2·96	2·80
Tail	94·0	87·0	Breadth at M^3 (B.M.)	8·91	8·90
Ear	No data		Length, M^{1-3}	5·24	5·30
Pes	21·8	20·5	P.C./B.L., as per cent	26·3	26·8
Basalar length (B.L.)	25·25	24·50	Z.B./B.L., as per cent	61·9	62·4
Zygomatic breadth (Z.B.)	15·78	15·25	P.L./B.L., as per cent	54·5	55·3
Postorbital constriction (P.C.)	6·55	6·55	B.M./B.L., as per cent	35·3	36·3
Palatalar length (P.L.)	13·79	13·50	P.C./Z.B., as per cent	41·0	43·0

mals in running about on the walls and ceilings of caves. In Victoria, evidence of cliff occupancy by *A. stuartii* was provided by several specimens trapped at Murrindal (eastern Victoria) and one at Glen Aire on the Otway Peninsula (south-western Victoria), in both cases at limestone cliffs.

Wakefield (1954) commented on the climbing ability and speed of movement of *A. stuartii* (again as *A. flavipes*), and recorded several observations of individuals abroad in full daylight. The species is normally nocturnal and, like *A. flavipes*, its usual food is insects, obtained partly about tree trunks and limbs and partly about logs and amongst ground litter.

A. s. adustus is known only from Ravenshoe and near Townsville, in north-eastern Queensland, and it is presumably an animal of the tropical rainforests.

IX. PLASTIC CHARACTERS OF ANTECHINUS STUARTII

The general comments on *A. flavipes* at the beginning of Section IV apply equally well to *A. stuartii*, as the external differences between them, except in pelage colour, are not very obvious. In the following notes attention has been drawn to the major points of distinction by which *A. stuartii* can be recognized.

(a) *Body measurements*

The body measurements of a series of 123 males and 63 females are summarized in Table 10. Specimens from all parts of the species range are represented but the bulk of the series is from Loch Valley (38°00′ S., 145°33′ E.) in eastern Victoria. Details of the latter are included separately (Table 11) to show the variation in a relatively large sample from one locality.

It is apparent from these data that the body proportions of both sexes are similar and that males are larger than females in head-body, tail and pes length. This sexual dimorphism is of high statistical significance ($P<0{\cdot}001$ in each case). If these same data are compared with those of *A. f. flavipes* (Table 1) it is seen that *A. stuartii* is a much smaller animal with a proportionately longer tail.

TABLE 13

Cranial measurements of *Antechinus stuartii stuartii* (total series)
Measurements in millimetres

		Range	Mean ± S.E.	Standard Deviation
Basalar length (B.L.)	122 ♂♂	21·40–27·70	24·33 ± 0·11	1·185
	63 ♀♀	21·35–26·20	23·35 0·13	1·062
Zygomatic breadth (Z.B.)	120 ♂♂	14·20–17·40	15·61 ± 0·06	0·662
	59 ♀♀	13·50–16·40	14·97 0·10	0·751
Postorbital constriction (P.C.)	134 ♂♂	5·90– 7·45	6·68 ± 0·02	0·231
	70 ♀♀	5·85– 7·00	6·38 0·03	0·234
Palatalar length (P.L.)	130 ♂♂	11·50–15·65	13·39 ± 0·06	0·630
	67 ♀♀	11·65–14·60	12·94 0·08	0·688
Anterior palatine foramen	133 ♂♂	2·15– 4·50	2·71 ± 0·04	0·425
	66 ♀♀	2·25– 4·60	2·68 0·05	0·432
Breadth at M^3 (B.M.)	130 ♂♂	7·90– 9·95	8·70 ± 0·04	0·440
	70 ♀♀	7·70–10·00	8·64 0·06	0·505
Length, M^{1-3}	128 ♂♂	4·50– 5·70	5·07 ± 0·03	0·289
	70 ♀♀	4·50– 5·60	5·09 0·03	0·292
P.C./B.L., as per cent	121 ♂♂	23·2 –30·7	27·5 ± 0·12	1·28
	63 ♀♀	24·5 –30·4	27·4 0·16	1·28
Z.B./B.L., as per cent	115 ♂♂	60·3 –68·7	64·1 ± 0·14	1·55
	57 ♀♀	60·0 –69·2	64·2 0·28	2·13
P.L./B.L., as per cent	121 ♂♂	51·1 –57·5	54·6 ± 0·09	0·98
	62 ♀♀	53·3 –57·2	55·3 0·12	0·93
B.M./B.L., as per cent	117 ♂♂	32·9 –38·5	35·7 ± 0·09	0·96
	63 ♀♀	34·6 –39·3	37·0 0·15	1·20
P.C./Z.B., as per cent	119 ♂♂	37·6 –46·2	42·9 ± 0·16	1·79
	58 ♀♀	38·1 –47·6	42·7 0·24	1·84

(b) *Manus and pes*

The feet of a series of 78 specimens from Victoria and New South Wales were examined. The appearance of the palmar and plantar surfaces are similar to those of *A. flavipes* (Figure 5). The chief difference between the feet of these two species lies in the frequency of fusion of the first interdigital and inner metacarpal (-tarsal) pads. Fusion occurs more frequently in *A. stuartii*, as shown by Table 5.

As in *A. flavipes*, several discrete and conspicuously large granules are normally present between the outer metatarsal pad and the heel. Another of similar size is often to be found near the outer margin of the third interdigital pad. In some 10 per cent of cases this latter structure is strongly striated, forming a super-numerary pad on the same transverse line as the interdigital pads but not exceeding half their size. Super-numerary pads were not observed on the comparatively few specimens available of *A. flavipes*.

The strong development of striated pads in *A. flavipes* and *A. stuartii* appears to be an adaptation to their arboreal habits and is in marked contrast to the condition seen in *A. swainsonii* and *A. minimus*, both of which are terrestrial in habit (Wakefield and Warneke, 1963). The foot pads of both *A. flavipes* and *A. stuartii* are large and prominent, and only in the

TABLE 14

Cranial measurements of *Antechinus stuartii stuartii* (Loch Valley series)
Measurements in millimetres

		Range	Mean ± S.E.	Standard Deviation
Basalar length (B.L.)	52 ♂♂	21·40–24·55	23·55 ± 0·08	0·585
	12 ♀♀	21·35–23·05	22·03 0·12	0·432
Zygomatic breadth (Z.B.)	51 ♂♂	14·45–16·10	15·25 ± 0·06	0·423
	11 ♀♀	13·50–14·85	14·27 0·14	0·465
Postorbital constriction (P.C.)	59 ♂♂	6·30– 7·10	6·68 ± 0·03	0·194
	12 ♀♀	6·00– 6·70	6·36 0·06	0·208
Palatalar length (P.L.)	57 ♂♂	11·50–13·65	12·84 ± 0·05	0·380
	12 ♀♀	11·65–12·50	12·08 0·09	0·295
Anterior palatine foramen	58 ♂♂	2·15– 3·20	2·63 ± 0·03	0·205
	12 ♀♀	2·25– 2·90	2·52 0·05	0·182
Breadth at M^3	55 ♂♂	7·90– 8·80	8·36 ± 0·02	0·180
	12 ♀♀	7·70– 8·65	8·05 0·07	0·245
Length, M^{1-3}	57 ♂♂	4·50– 5·10	4·84 ± 0·02	0·140
	12 ♀♀	4·50– 5·30	4·73 0·05	0·170
P.C./B.L., as per cent	52 ♂♂	26·8 –30·7	28·4 ± 0·11	0·80
	12 ♀♀	27·5 –30·4	28·9 0·25	0·88
Z.B./B.L., as per cent	48 ♂♂	61·2 –67·7	64·6 ± 0·22	1·53
	11 ♀♀	62·0 –67·5	64·8 0·54	1·79
P.L./B.L., as per cent	52 ♂♂	51·1 –56·1	54·5 ± 0·13	0·95
	11 ♀♀	53·7 –56·1	54·9 0·24	0·81
B.M./B.L., as per cent	49 ♂♂	33·9 –37·6	35·5 ± 0·10	0·73
	12 ♀♀	35·3 –39·3	36·6 0·37	1·28
P.C./Z.B., as per cent	50 ♂♂	41·6 –46·2	43·9 ± 0·18	1·25
	11 ♀♀	42·8 –47·6	44·5 0·40	1·32

latter is there a high degree of fusion on the pes. Here fusion is not accompanied by a reduction in size, on the contrary, the compound pad may be even slightly larger than the combined length of typical separate pads.

The structure of the claws also appears to be related to habit. In both *A. flavipes* and *A. stuartii* they are light, yet strongly curved and very sharp, and are thus well suited to climbing (see Figure 5).

(c) *Pelage*

The pelage of *A. stuartii* is noticeably softer than that of *A. flavipes*, evidently because the guard hairs are less strongly developed and hence do not affect the overall texture to the same degree. In other respects the physical components of the pelage of the two species are similar.

In dorsal colouration *A. stuartii* is a dull drab brown, lightly flecked with fawn, the latter colour occurring as a subterminal band in the main pile. Antero-posterior differentiation is absent or scarcely developed. In some specimens the ventrum is pale grey with a tinge of fawn; in others it is more strongly tinged across the midbelly with a pale brown. Ear patches and orbital crescents are absent or faint and ill-defined. The dorsal surface of both manus and pes is drab brown to grey brown. The dorsal surface of

the tail near the base is brown, flecked with fawn; below it is greyish fawn.

Some specimens are noticeably darker in colour, and in general this appears to be related to habitat. The description given above applies to specimens from coastal areas and dry sclerophyll forests. Dark specimens with warmer tonings were taken in wet sclerophyll forests in central Victoria, at Mount Macedon (3300 feet), Mount Arnold (4300 feet) and Loch Valley (1900 feet).

The few skins of *A. s. adustus* that we examined could not be distinguished from these latter specimens.

X. SKULL AND DENTITION OF ANTECHINUS STUARTII

Apart from significant size differences, the skull of *A. stuartii* closely resembles that of *A. flavipes* (see Figures 6 and 8). However, when fully adult series are compared, the bones of *A. stuartii* skulls appear lighter and the supra-occipital crests are much less developed than in *A. flavipes*. The form and structure of the bulla are the same in both species.

The respective dentitions, including the deciduous premolars, are identical except that the incisor gradient $I^2 > I^3 > I^4$ is less marked in *A. stuartii*; in some specimens the upper incisors are equal in size.

Measurements and proportions of a series of skulls of *A. stuartii* from Victoria, New South Wales and south-eastern Queensland are set out in Table 13. Data on a series from Loch Valley are included separately to show variation in a relatively large sample from one locality (see Table 14).

The skulls of both sexes have similar proportions, but those of males average about 4 per cent larger in linear dimensions than those of females. The sexual differences in skull length and width are both of high statistical significance ($P<0.001$ in each case).

There is some indication from the data that the length of the molar row diminishes in a metrical cline from Queensland to Victoria, as 11 specimens from Mount Glorious (27°20′ S., 152°45′ E.) in Queensland averaged 5.50 ± 0.05 mm.; 10 specimens from Mount Irvine (33°30′ S., 150°27′ E.) in the Blue Mountains of New South Wales 5.33 ± 0.04 mm.; 7 specimens from Argalong (38°18′ S., 148°26′ E.) 5.29 ± 0.04 mm.; and the Loch Valley series 4.83 ± 0.02 mm. However, as the northern and south-western extremities of the species range are each represented by only a few specimens, the full range of this clinal variation is unknown.

Comparison of Tables 13 and 6 show that the skull and teeth of *A. stuartii* are much smaller than those of *A. flavipes*, but, in our interpretation of speciation within *Antechinus*, difference in skull size is not considered to be of primary importance. However the two species differ considerably in one cranial proportion; in relation to length, the skull of *A. stuartii* is slightly narrower in zygomatic breadth, but is also much broader in post-orbital width (see Z.B./B.L. and P.C./B.L. in Tables 13 and 6). In these two tables the proportion Postorbital Constriction/Zygomatic Breadth is given, and in this the difference between the two species is of a high order of significance ($P<0.001$).

XI. BREEDING CONDITION OF ANTECHINUS STUARTII

Females. Marlow (1961) gave very full descriptions of the external changes associated with breeding in this species, but under the name *A. f. flavipes*. These changes are similar to those noted in other species of *Antechinus* (Wakefield and Warneke, 1963; and

TABLE 15

Body measurements of *Antechinus godmani*

Measurements in millimetres

		Range	Mean ± S.E.	Standard Deviation
Head–body	13 ♂♂	122 –160	143·0 ± 2·86	10·33
	25 ♀♀	90 –133	121·9 1·79	8·94
Tail	13 ♂♂	105 –146	123·8 ± 3·02 *(87%)	10·90
	25 ♀♀	86 –115	104·1 1·64 (86%)	8·18
Ear	3 ♂♂	16 – 19	17·3 (12%)	
	4 ♀♀	14·5– 16·5	15·5 (13%)	
Pes	13 ♂♂	21 – 27	24·2 ± 0·30 (17%)	1·74
	25 ♀♀	19 – 24	21·5 0·33 (18%)	1·64

* Per cent of head–body length.

this paper). The timing of events in Marlow's captive colony is similar to that which may be deduced from Victorian field records, as follows:

Birth occurs at about mid-September. The actual date was recorded in one instance where a female gave birth in captivity, on September 14-15, seventeen days after capture. Gestation in this species takes 32 to 34 days (Marlow, 1961: 208; and observations by R.M.W.).

The young remain attached to the nipples for about five weeks, and subsequent to October 20 the pouch area of all lactating females trapped was found unoccupied. A female, FWD. No. D.449, trapped on December 9, 1962, was still lactating, indicating that the young are suckled until early December at least.

The number of nipples in *A. stuartii* varies from locality to locality, but appears to be constant in certain areas. For example, all females from the Cape Otway and Portland areas of south-western Victoria had 6; those from the Grampians had 8; from the Ballarat area 10; from the ranges east of Melbourne (including Loch Valley) 8; and from north-eastern Gippsland (Murrindal and Wulgulmerang) 10. To date all reliable counts from New South Wales specimens have been 8. Two females of *A. s. adustus* from Mount Spec, near Townsville, had 6 and 8 nipples respectively.

Males. The comments on *A. flavipes* in Section VI apply also to *A. stuartii.*

XII. PLASTIC CHARACTERS OF ANTECHINUS GODMANI

(a) *Body measurements*

Thirty-eight specimens were available to us, all of which were collected in or near the Ravenshoe district on the Atherton Tableland, close to the type locality. Thomas's published measurements of the type (Thomas, 1923), an adult male, have been included in Table 15, as these were the only other reliable data on an authentic specimen that was not seen by us. The statistical analysis of head-body and pes length in this species, made by Horner and Taylor (1959), was based on a series of specimens which we have since examined and found to include *A. flavipes* as well as *A. godmani.* These authors accepted Tate's evaluation of *godmani* as a subspecies of *A. flavipes* (Tate, 1952) but drew attention to the fact that Tate also

recognized *adustus* (actually a form of *A. stuartii,* see Section VII)—which occurs sympatrically with *A. godmani*—as a subspecies of *A. flavipes.*

Table 15 shows a marked disparity between the sexes in body size, which is in keeping with the sexual dismorphism noted in other *Antechinus* (Troughton, 1941: 26; Horner and Taylor, 1959; Marlow, 1961; Wakefield and Warneke, 1963).

As far as can be judged from the series available, *A. godmani* is the largest species of *Antechinus* in eastern Australia (see also Thomas, 1923). It is slightly larger than the Cape York form of *A. flavipes* and is considerably larger than the North-east Queensland form of that species.

(b) *Manus and pes*

In structure the manus and pes are closely comparable with those of *A. flavipes* and *A. stuartii.* However, as in the latter, there is a relatively high frequency of fusion of the first interdigital and inner metatarsal pads of the pes (see Table 5). In eleven of twenty-six specimens these pads were fused on both feet and in four of the others on one foot only. The first interdigital and inner metacarpal pads of the manus were distinctly separate in all twenty-six specimens.

On each of the pes of ten specimens, three small striated super-numerary pads were noted. These were on the sole, immediately below and in line with the second, third and fourth interdigitals respectively—an occurrence without parallel in the other *Antechinus* examined by us.

The form of the claws is similar to that of *A. flavipes* and *A. stuartii.*

(c) *Pelage*

The main pile is moderately fine in texture and the guard hairs, though profuse, are relatively short. The general dorsal colour is a subdued cinnamon brown, with conspicuous glints of fawn due to a sub-terminal band of that colour in the main pile; the basal zone is slate grey. A sheen is imparted to the whole by the guard hairs, which are glistening black, fading to light brown at the tips. Antero-posterior differentiation in dorsal colour appears to be stronger in males than in females, with the rump noticeably warmer in tone than the head and upper back. In his description of the species, Thomas (1923) made no distinction between the sexes on this point. In both sexes the fur of the ventrum is a uniform greyish fawn at the tips and slate grey beneath.

Orbital crescents and basal ear patches are lacking. The sides of the face, especially at the angle of the jaw, are rufescent. The dorsal surface of both manus and pes is ochraceous brown or cinnamon brown. The tail is unlike that of any other eastern Australian *Antechinus.* The dorsal surface is almost naked, having only a sparse covering of short adpressed brown hairs, while on the underside the hairs are longer and more dense, and form a ventral crest which extends beyond the tail tip.

XIII. SKULL AND DENTITION OF ANTECHINUS GODMANI

Because this species has been confused with *A. flavipes* (see Section XII), the following comments emphasize those features of the skull and dentition which are of diagnostic importance. Other features may be seen in Figures 6 and 9.

On the average the skull is larger than that of *A. flavipes,* is narrower in relation to length and has a proportionately longer rostrum. The postorbital constriction is noticeably broader in relation to zygomatic breadth and the frontal region is depressed as in *A. swainsonii.* The anterior palatine

TABLE 16

Cranial measurements of *Antechinus godmani*
Measurements in millimetres

		Range	Mean±S.E.	Standard Deviation
Basalar length (B.L.)	7 ♂♂	30·00–32·85	31·18±0·38	1·000
	7 ♀♀	27·70–29·60	28·24 0·29	0·696
Zygomatic breadth (Z.B.)	6 ♂♂	17·55–19·75	18·73±0·27	0·669
	8 ♀♀	16·20–17·40	16·82 0·14	0·396
Postorbital constriction (P.C.)	8 ♂♂	7·55– 7·95	7·76±0·04	0·118
	8 ♀♀	7·40– 8·05	7·70 0·07	0·185
Palatalar length (P.L.)	7 ♂♂	16·50–18·30	17·20±0·22	0·590
	8 ♀♀	15·55–16·75	16·02 0·16	0·463
Anterior palatine foramen	6 ♂♂	2·50– 3·00	2·81±0·09	0·216
	9 ♀♀	2·25– 3·15	2·71 0·11	0·352
Breadth at M^3 (B.M.)	7 ♂♂	9·65–10·65	10·24±0·13	0·351
	8 ♀♀	9·60–10·30	9·92 0·07	0·208
Length, M^{1-3}	8 ♂♂	5·95– 6·25	6·11±0·04	0·118
	8 ♀♀	5·80– 6·30	6·03 0·06	0·159
P.C./B.L., as per cent	7 ♂♂	23·6 –25·7	25·0 ±0·26	0·69
	7 ♀♀	25·8 –28·4	27·2 0·34	0·91
Z.B./B.L., as per cent	7 ♂♂	58·1 –61·5	59·6 ±0·51	1·36
	7 ♀♀	58·4 –61·2	59·7 0·43	1·17
P.L./B.L., as per cent	7 ♂♂	53·2 –56·1	55·2 ±0·39	1·04
	7 ♀♀	56·0 –58·4	56·7 0·29	0·77
B.M./B.L., as per cent	7 ♂♂	31·6 –34·0	32·9 ±0·30	0·80
	7 ♀♀	33·6 –36·2	35·1 0·37	0·99
P.C./Z.B., as per cent	6 ♂♂	39·2 –43·5	41·5 ±0·53	1·31
	8 ♀♀	43·7 –48·1	45·8 0·54	1·52

foramina are short. The bulla is similar to that of *A. flavipes* and *A. stuartii* in structure, but the inflation of the alisphenoid does not extend as far anteriorly.

Of the incisors, I^1 is of medium size, only slightly proödont and separated from I^2 by a slight diastema; I^{2-4} are sub-equal, compressed laterally and not crowded together. The upper premolars are compressed laterally and are not separated by interspaces. M^4 has a small distinct metacone. I_3 bears a small accessory cusp on the buccal aspect near the heel, which slightly overlaps the canine.

Deciduous teeth were not found in any of the skulls examined by us.

In the outline of the skull as viewed from above; in the form and position of I^1; in the presence of the accessory cusp on I_3 and a metacone on M^4, *A. godmani* shows a marked resemblance to *A. minimus* (see Wakefield and Warneke, 1963: 218).

XIV. BREEDING CONDITION OF ANTECHINUS GODMANI

Females. On each of eight skins of females obtained in late November-December, 1921, the pouch area was greatly enlarged and most of the nipples were elongated, indicating that young were still being suckled. The appearance of the mammary region was essentially the same as that of other species at the same stage of development, and the period of year

when they were captured corresponds to the time of lactation in other species.

In four specimens 3 pairs of nipples were plainly visible, while in each of the other four specimens one nipple had regressed to a very small size but in each case was readily located by reference to the symmetry of the others. Thus the nipple number of *A. godmani* is 6.

Males. No information was available to us.

XV. APPENDIX

Amended distribution of *Antechinus minimus maritimus.*

Since the publication of distributional data (Wakefield and Warneke, 1963), the following additional specimens of *A. m. maritimus* have been located:

FWD. No. D.208. ♀. Anglesea, Victoria. 28 Jan. 1957.

FWD. No. D.582. ♂. Between Lighthouse Track and Waterloo Bay, Wilson's Promontory, S.E. Victoria. 5 Jan. 1965.

FWD. No. D.647. Glennie Island, S.E. Victoria. 14 June 1966.

These records treble the known range of the mainland Australian race of *A. minimus.*

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